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The functional significance of multiple nest-building in the Australian Reed Warbler *Acrocephalus australis*

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The vast majority of bird species build a nest in which to breed. Some species build more than one nest, but the function of most multiple nest-building remains unclear. Here we describe the unusual nest-building behaviour of the Australian Reed Warbler *Acrocephalus australis*, and test experimentally the hypotheses that multiple nest-building is related to individual condition or territory quality, and plays a role in mate assessment. Australian Reed Warblers built two types of nest structures: 'type I' nests, which were used for eggs and nestlings, and 'type II' nests, which were structurally distinct from type I nests, did not support eggs, nestlings or adults and were not essential for successful breeding. The number of type II nests built in each territory varied. Type II nests were only built before breeding had commenced in a territory and females were not observed participating in their construction, supporting a role in female mate choice. Birds provided with supplementary food built significantly more type II nests than control birds. However, supplementary-fed birds did not have greater pairing success, and the addition of further type II nests to territories did not increase the pairing rate or type II nest construction in those territories. There was no relationship between the presence of type II nests and either reproductive success or likelihood of nest predation. We discuss the implications of these results in light of previous suggestions regarding the function of multiple nest-building in birds.

Nest-building is an essential activity for successful reproduction in most birds, and many species expend considerable time and energy in the construction of one or more elaborate nests for breeding (Verner & Engelsen 1970, Collias & Collias 1984, Metz 1991). There is evidence that both the selection of a nest-site and the quality of a nest can have important effects on breeding success (Thompson & Furness 1991, Hoi *et al.* 1994, 1996, Weidinger 2002). Although most species typically build only one nest per breeding attempt, some species simultaneously build more nests or nest-like structures than are used for breeding (e.g. Verner & Engelsen 1970, Garson 1980, Savalli 1994, Friedl & Klump 1999). To date, there has been remarkably little empirical work on this unusual behaviour, but several hypotheses have been proposed to explain the adaptive significance of multiple nest-building. These include: (1) to reduce

excess energy (Forbush 1929), (2) to practise nest-building (Hunter 1900), (3) to outline territory boundaries (Allen 1923), (4) to provide shelter for adults or fledglings (Verner 1965) and (5) to act as decoys to reduce predation (Shufeldt 1926, Leonard & Picman 1987). However, the most commonly invoked hypothesis is that of mate attraction (e.g. Verner & Engelsen 1970, Collias & Collias 1984, Evans & Burn 1996, Soler *et al.* 1998, Brouwer & Komdeur 2004). If this is the case, individuals might signal their current condition or the quality of their territory (e.g. food availability, nest-site quality or the absence of nest predators) through constructing multiple nests (e.g. Leonard & Picman 1987, Moreno *et al.* 1994, Savalli 1994, Evans & Burn 1996, Kusmierski *et al.* 1997, Friedl & Klump 2000). In this way, even non-breeding nests may be considered as (non-bodily) ornaments in the same way as other secondary sexual characters (Andersson 1994). Moreover, when both sexes participate in nest-building it may be a sexually selected display that allows each sex simultaneously to gain reliable information on the condition or quality

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of the other (Soler *et al.* 1998), and may function in mutual mate assessment or pair bonding.

The Australian Reed Warbler *Acrocephalus australis* arrives at breeding sites in southern Australia from September to December. Males arrive before females and defend small breeding territories throughout the breeding season (Cramp 1992, M. Berg, J. Welbergen & R. Kats unpubl. data). Pair-bonds typically persist throughout the season and the social breeding system is primarily monogamous, although polygyny and extra-pair fertilizations can occur (Brown & Brown 1986, J. Welbergen & M. Berg unpubl. data). Nests are constructed in beds of Common Reed *Phragmites australis*, where potential nest-sites are extremely abundant. The birds frequently build more nest structures than are actually used for breeding (Courtney-Haines 1991, this study); however, in contrast to similar systems well documented previously, there is a clear and consistent structural difference between the nests that are used for breeding ('type I nests', Fig. 1a) and the nests that are not used for breeding ('type II nests', Fig. 1b). Type I nests are typically supported by three or more closely placed reed stems and have a distinct cup shape suitable for containing a clutch or brood. Type II nests are much smaller, rudimentary structures that are always built on only two reed stems and which, lacking a cup shape, are not suitable for egg-laying, or for the shelter of offspring or adults (see Verner 1965). Several broods are usually attempted in a season, with a new type I nest being built for each breeding attempt (Brown & Brown 1986, this study).

In this study, we describe the unusual nest-building behaviour of the Australian Reed Warbler, which has not been documented in detail previously. As has commonly been proposed in other species (e.g. Verner & Engelsen 1970, Evans & Burn 1996), previous workers have suggested that multiple nests may be built by male Australian Reed Warblers for mate attraction purposes (so-called 'cock nests', Courtney-Haines 1991). We predicted that if type II nests function in mate assessment, these nests will only be built during the period of pair formation, whereas if they have a different function or are by-products of type I nest-building attempts they should appear throughout the breeding cycle or during re-nesting attempts. We also conducted two experiments designed to examine further the functional significance of multiple nest-building in this species, with particular attention to a potential role of type II nests in mate and/or territory assessment and pair formation ('sexual selection' hypothesis). First, we conducted a supplementary-feeding experiment to examine the role of territorial food availability on nest-building. If the construction of multiple nests is energetically constrained, the number of type II nests built by an individual or pair may be a signal of condition or territory quality (Zahavi 1987). Secondly, we performed a nest-addition experiment (Leonard & Picman 1987) using artificial type II nests (Fig. 1c). With this experiment we could test directly the relationship between type II nest number or density and subsequent nest-building or pairing success, without the confounding effects of associated



Figure 1. Type I nest (a) and type II nest (b) of an Australian Reed Warbler, and artificial type II nest (c) used in the nest-addition experiment.

variation in nest quality, individual quality or territory quality.

MATERIALS AND METHODS

Study area and data collection

The study was conducted on a colour-banded population of Australian Reed Warblers in 10 ha of Common Reed at Edithvale-Seaford Wetlands (38°02'S, 145°07'E), Australia. The study was conducted from October 2000 to January 2001, the main breeding season of the Australian Reed Warbler. We found nests by searching systematically through the reeds every 1–2 weeks on 5-m transects, parting the vegetation carefully to minimize disturbance. Nests were classified as either of type I or type II, marked with a small piece of green or yellow plastic tape on a nest support stem (to match the surrounding vegetation and allow exact re-location of the nest even if it disappeared) and located with a hand-held satellite global positioning system (Garmin GPS 12®) to a precision of < 5 m. Type I nests were considered active if they contained a clutch or brood, or if their construction had been completed since last searching the area (clutches are always initiated within 1 week of nest completion, J. Welbergen & M. Berg unpubl. data). All type I nests were monitored every 2 days for changes in their contents and the appearance of new nests within 10 m (0.04 ha). This arbitrary area centred around a type I nest was chosen as a compromise intended to incorporate most of the surrounding territory but to minimize overlap with neighbouring territories. It is very difficult to make direct behavioural observations and to map large numbers of territories accurately in this species because of its cryptic habits, the small size of the territories, and the dense and homogeneous vegetation that it inhabits. Clutches were considered complete when incubation had commenced and more than 1 day had elapsed since the laying of the previous egg (eggs are laid on consecutive days, Welbergen *et al.* 2001). Nests were considered predated when eggs disappeared, when eggshells were found in the nests or when nestlings disappeared before 9 days of age (fledging occurs at approximately 10–11 days of age, Berg 1998).

Observations of nest-building were made with 8-mm video cameras (Sony Handycam) on tripods 1–3 m from the nests. The video cameras were covered with hessian bags, which are known substantially to reduce the disturbance caused to the breeding birds

(our pers. obs.). Nine type I nests were filmed in the construction stage ($3.09 \text{ h} \pm 0.02 \text{ sd}$ each), and 18 newly discovered type II nests were filmed ($02.33 \text{ h} \pm 0.03 \text{ sd}$ each). From these videos we recorded all nest-building activity by both sexes. We also marked some nest material in each of five type II nests with spray paint or an indelible marker to determine whether this material was later used for the construction of other nests.

Supplementary-feeding experiment

In order to test whether the construction of type II nests is energetically constrained and may therefore indicate territory quality or individual condition, we conducted a supplementary-feeding experiment (see also Berg *et al.* 2005). Two approximately rectangular, equally sized 'sections' of reed, each of c. 300 m × 50 m and situated on opposite sides of a lake (c. 500 m apart), were selected on the basis of their homogeneity and subjective comparability in reed structure and proximity to water (in order to minimize natural differences in food availability and nesting sites between the treatments). Each section was divided into two equal 'areas' which were randomly assigned to either receive supplementary feeding or to serve as a control. In each area, we made parallel transects spaced 20 m apart and perpendicular to the lake/reed edge. Plastic trays (20 cm diameter, 3 cm deep, supported c. 1 m high on a bamboo pole) were placed every 20 m along the transects in the supplementary-feeding areas (a typical breeding territory size is at least 20 m in diameter, M. Berg & J. Welbergen unpubl. data). Each tray was filled with c. 30 g of live blowfly maggots (*Calliphora* sp. larvae, Ritebait, Australia) in processed bran or rice husks every other morning at approximately 09:00 h AEST; 30 g represents approximately 135 kJ (at 4.5 kJ/g, Inaoka *et al.* 1999), which is expected to be > 1.25 times the field metabolic rate of an Australian Reed Warbler (c. 18 g) when raising nestlings (90 kJ/day, Dawson & O'Connor 1996), assuming a 75% assimilation efficiency (Castro *et al.* 1989). Maggots were unable to escape from the trays. Supplementary feeding was carried out from 7 October to 7 December. When feeding, we also walked along the transects in the control areas to generate equal disturbance. Individuals in these areas were caught in mist-nets and colour banded for individual identification. All territories in the supplementary-fed and control areas were accurately mapped and monitored during November and December (described in Berg *et al.*

2005). Remote video observations at random feeding trays ($2.75 \text{ h} \pm 0.90 \text{ sd}$ each, $n = 7$) revealed that Reed Warblers of both sexes routinely consumed the supplementary food and that no other bird species fed on the maggots. The maggots were usually largely depleted within several hours and were always gone by the following day. This supplementary-feeding treatment is known also to increase incubation attendance (Eikenaar *et al.* 2003), male song rate (Berg *et al.* 2005) and nestling food provisioning rate (J. Welbergen & M. Berg unpubl. data).

Type II nest-addition experiment

If supplementary-fed birds were induced to build more type II nests, we could test to some extent the role of type II nests in pairing success. However, the supplementary-feeding experiment alone is not adequate to test for a direct role of type II nests on mate attraction, because female settlement could be affected by the supplementary food directly or indirectly through changes in other behaviours, such as singing (Berg *et al.* 2005). In order to investigate further the potential role of type II nests in mate attraction, we conducted an artificial nest-addition experiment. Between 27 November and 6 December, during the main nesting period, we randomly selected 11 pairs of quadrants throughout the study site, excluding the supplementary-feeding areas and their control areas. Each quadrant was centred around the average position of a singing male observed for approximately 30 min (considered the approximate 'centre' of the territory), and measured $20 \times 20 \text{ m}$ (0.04 ha) in order largely to encompass the area of a typical breeding territory. Such a quadrant was considered suitable for the experiment if it did not contain any type I nests, thus indicating that the males were almost certainly unpaired (old type I nests almost always persist throughout the season, see Results). The quadrants forming most pairs were located approximately 50 m apart, and always at least 5 m apart to reduce interference. Quadrants were randomly assigned to either the experimental or the control group. In the centre of each experimental quadrant, we constructed a cluster of ten randomly placed artificial type II nests (Fig. 1c). The artificial nests were made from hessian string (a material which resembled the natural nesting material and is readily used by Australian Reed Warblers in nest construction, see Results) and strongly resembled natural type II nests except that they were resistant to destruction. The heights (1–2 m) and distances

between the nests (1–2 m) were in line with those which may occur naturally, but the number in experimental territories now substantially exceeded the observed natural range for such an area (0–3). We checked all experimental and control quadrants (thereby equalizing disturbance between experimental and control quadrants) 2 days, 1 week, and 4 weeks after the onset of the individual experiments for the appearance and status of new nests and for the condition of the artificial type II nests.

Data analyses

Two variables were used to quantify the relative density of type II nests: the distance from a type I nest to the nearest type II nest in the study area, and the number of type II nests within 10 m of a type I nest. These two measures were strongly correlated ($r = -0.402$, $n = 224$, $P < 0.001$), and yielded qualitatively similar results in the analyses; therefore, only results from the former are presented because this measure does not invoke an estimation of territorial area. When relating rates of predation and clutch completion to the presence of type II nests, data from both supplementary-feeding and control areas were pooled as there were no differences between these areas in predation rate or probability of clutch completion (see Results).

All statistical tests were performed using SPSS 11 for Windows (SPSS Inc., 1999) and followed the methods of Sokal and Rohlf (1995). We used non-parametric tests when data were not normally distributed or variances were unequal. All proportions were arcsine transformed before testing. All P -values reported are two-tailed and considered significant at $P < 0.05$.

RESULTS

Patterns of nest-building, placement and usage

Throughout the study site we located 357 nests, of which 250 (70%) were originally classified as type I and 107 (30%) as type II. Each estimated territory contained 0–3 type II nests. One type I nest was built for each breeding attempt, and most territories ultimately contained more than one type I nest from multiple breeding attempts. Three type I nests (1%) were reclassified as type II nests during subsequent visits, which may represent misclassification of type I nests after destruction by predators. Twelve type II

nests (11%) were subsequently reclassified as type I nests, which is probably due to type I nests being built on the position of an existing type II nest or, less commonly, a misclassification of a type I nest in construction as a type II nest. New type I and type II nests in construction could be identified easily because they were invariably wet and contained fresh, green vegetation; Reed Warblers apparently wet material before adding it to nests (Courtney-Haines 1991). Nest-building was observed on four of the nine type I nests filmed in the construction stage, and in all four cases both the male and the female were observed contributing regularly to nest-building. Construction of type I nests was always completed within 3 days and, once completed, no further material was added to type I nests for the remainder of the breeding attempt. Construction of type II nests appeared to occur more rapidly. Of the 18 new type II nests filmed, one recording showed a male inspect the nest briefly and leave. On another three recordings male Reed Warblers were observed to sing loudly and manipulate the nest material, although in no cases was material added to or taken away from the nest. No other displays were observed at type II nests, and no females were observed in contact with type II nests.

After the observed completion of type I nests ($n = 151$), new type II nests were never observed to be built within 10 m of these nests. Marked nest material from three type II nests was found in type I nests in the same territory. In addition, Warblers readily used artificial material present in their territory for nest construction (particularly hessian from the bags used to disguise video cameras). Although some type II nests remained intact throughout the season, most were destroyed or decayed and gradually disappeared after a short period of time. It was usually difficult to determine whether damaged type II nests had been actively destroyed by Reed Warblers. Type I nests persisted throughout the breeding season, except in rare cases ($< 10\%$) when they were apparently destroyed by a large predator (these include domestic cats and gallinules, Cramp 1992). We observed no cases where type I nests appeared to have decayed or fallen down over the course of a single season. Type I nests were never re-used after a previous clutch.

The presence of type II nests did not correlate with any measure of reproductive success. There were no significant correlations between clutch size, the number of hatchlings or the number of fledglings (excluding predated nests) and the distance to the

Table 1. Numbers and densities (per hectare and per male/territory) of type I and type II nests and males in supplementary-fed and control areas (chi-squared test). Number of males was based on territory mappings (see Berg *et al.* 2005).

	Supplementary-fed	Control	χ^2	<i>P</i>
Males	$n = 28$	$n = 22$		
per ha	21.78	17.11	0.641	0.423
Type I nests	$n = 23$	$n = 19$		
per ha	17.89	14.78	0.273	0.602
per male	0.82	0.86	0.026	0.872
Type II nests	$n = 21$	$n = 7$		
per ha	16.33	5.44	5.762	0.016
per male	0.75	0.32	4.613	0.032
per Type I	0.91	0.37	4.102	0.043

nearest type II nest ($r = 0.112$, $n = 139$, $P = 0.187$; $r = 0.180$, $n = 85$, $P = 0.099$ and $r = 0.219$, $n = 55$, $P = 0.108$, respectively). Considering only nests where the predation status was known, there was no significant correlation between predation of type I nests and the distance to the nearest type II nest (logistic regression: $\chi^2_1 = 0.263$, $n = 171$, $P = 0.608$). Note that the conclusions of these analyses remain unchanged when the number of type II nests within 10 m is used instead of the distance to the nearest type II nest.

Supplementary-feeding experiment

The density of male territories was the same in supplementary-fed and control areas, as were the densities and number per male of type I nests (i.e. breeding attempts, Table 1). However, the densities of type II nests and the number of type II nests per male and per type I nest were significantly higher in supplementary-fed than in control areas (Table 1). To gain additional insight into the spatial distribution of nests, we also examined distances between nests in these areas. Accordingly, the mean distance from each type I nest to the nearest type II nest tended to be smaller in the supplementary-feeding areas than in the control areas, while the average distance between type II nests was significantly smaller in supplementary-feeding areas (Fig. 2). However, there was no effect of the supplementary-feeding treatment on the mean distances between type I nests and the closest type I nest, or between type II nests and the closest type I nest (Fig. 2).

There were no significant differences in the percentage of nests predated between the supplementary-fed

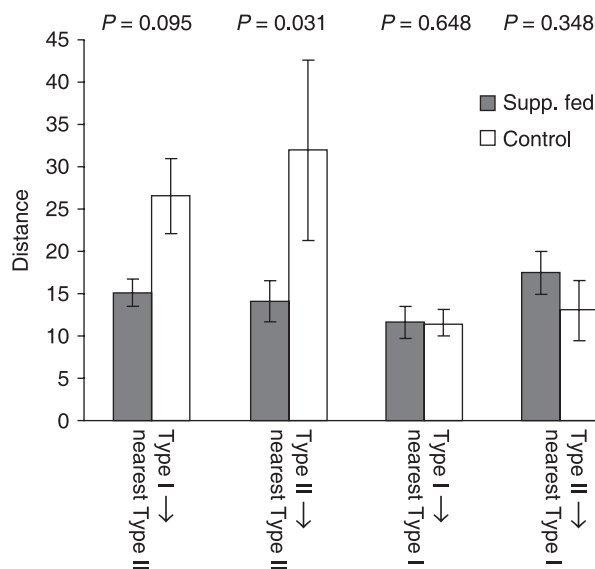


Figure 2. The mean distance (\pm se) of type I or type II nests to the nearest type I or type II nest in supplementary-fed and control areas (Mann–Whitney *U*-test). I \rightarrow II: $n = 23$ (supplementary-fed) and 19 (control); $Z = -1.669$, $P = 0.095$. II \rightarrow II: $n = 21$ (supplementary-fed) and 7 (control); $Z = -2.128$, $P = 0.031$. I \rightarrow I: $n = 23$ (supplementary-fed) and 19 (control); $Z = -0.456$, $P = 0.648$. II \rightarrow I: $n = 21$ (supplementary-fed) and 7 (control); $Z = -0.956$, $P = 0.348$.

areas (26%, $n = 23$), the control areas (32%, $n = 19$) and the rest of the study site (26%, $n = 208$) ($\chi^2_2 = 0.34$, $P = 0.845$), nor in the percentage of clutches completed once the construction of a type I nest was commenced (64, 76 and 80%, respectively; $\chi^2_2 = 3.58$, $P = 0.167$).

Type II nest-addition experiment

The birds appeared to treat the artificial nests as they do natural type II nests: in one case, a type I nest was constructed on top of an artificial type II nest, and in numerous cases small quantities of the hessian material from the artificial type II nests were used in the construction of type I nests. The numbers of type I and type II nests appearing during the 4 weeks after the onset of the experiment did not differ between treatment and control areas (Fig. 3). None of the males in these areas attracted more than one female during this period. This implies that the construction of both type I and type II nests, and commencement of breeding, occurred independently of the number of artificial type II nests already present on the territory.

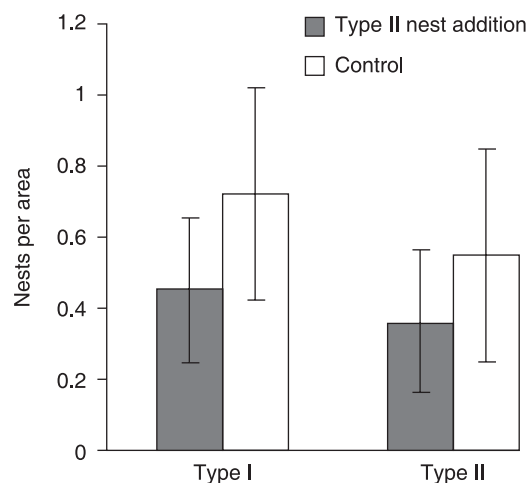


Figure 3. Mean (\pm se) number of type I nests and type II nests which appeared in experimental (ten artificial type II nests added) and control areas (20×20 m) within 4 weeks after the type II nest addition (paired *t*-test). Type I nests: $t_{10} = 0.671$, $P = 0.518$; type II nests: $t_{10} = 0.614$, $P = 0.553$.

DISCUSSION

Patterns of nest-building

Type II nests represented at least 27% of the nests built by Australian Reed Warblers during our study, even taking into account possible classification errors. For the most part, nests did not change status between type I and II. Together with the consistently different materials and structures between these nest types, this indicates that type I and type II nests fulfil distinct, independent roles in the breeding biology of this species.

Despite the large number of breeding attempts monitored, type II nests never occurred within 10 m of a completed type I nest (an area of 10 m either side of a type I nest (0.04 ha) would in most cases be sufficient largely to encompass the surrounding territory). This finding implies that no type II nests are built in a territory after pairing has taken place and the first breeding attempt has been made; this is the key distinction between this system and most multiple nest-building species studied previously, where males are often polygynous and typically continue to build nests even after acquiring a mate and commencing breeding activities. Accordingly, the function of type II nests is likely to involve the selection of a mate or breeding territory; it is unlikely to include the selection of a suitable nest-site because no type II nests were built during re-nesting attempts and

relatively few type I nests were built on the site of a type II nest. After construction, type II nests were either left to decay or were destroyed; several observations showed that Reed Warblers sometimes use the material for the construction of other nests.

Only males were observed in direct contact with type II nests, and type II nests occurred in the territories of unpaired males. These observations lead us to believe that males are probably responsible for the maintenance of type II nests with little involvement of females (Courtney-Haines 1991), a view consistent with the idea that type II nests are 'non-bodily' male ornaments. However, because of the small number and ambiguous nature of the type II nest-building observations, and given that both sexes are involved in the construction of type I nests in this species (Brown & Brown 1986, this study), it is still possible that type II nests could be used by both sexes to gain information on each other or the breeding site during pair formation (Soler *et al.* 1998).

We found no evidence that type II nests significantly affected reproduction post-pairing. We found no significant relationships between the presence of type II nests and nest predation, the probability of clutch completion or four measures of reproductive success for individual breeding attempts (clutch size, number of hatchlings, number of fledglings or predation). Some of these measures did tend to increase with decreasing proximity to a type II nest, which may reflect a lower breeding success with increasing local breeding density (Sinclair 1989).

Condition-dependent nest-building

If the construction of type II nests is functionally significant, then we predicted that birds freed from the energetic and temporal constraints of foraging would invest more in the construction of type II nests. Furthermore, if the construction of type II nests is constrained by food availability it could provide an honest signal for other individuals to assess the quality of the territory or the condition of the builder (Zahavi 1975, 1977, Andersson 1982).

In line with this expectation, Reed Warblers in supplementary-fed areas built significantly more type II nests, both per territory and per breeding attempt (i.e. type I nest). This led to correspondingly smaller distances between type II nests and between type I nests and the nearest type II nest (Fig. 2). These results were not related to nest predation, and supplementary-fed and control areas were specifically chosen in pairs to have as similar vegetation

structure and topography as possible. However, these results should be interpreted with some caution, because we used only two supplementary-fed and two control areas and it is possible that all individuals in a single area may not have been completely independent in terms of nest-building behaviour. Nevertheless, these data strongly suggest that the construction of type II nests is energetically or temporally constrained by food availability or foraging ability.

Previous research has shown that the energetic costs of nest-building in several bird species amounted to 1.5–4.9 times the basal metabolic rate (Dolnik 1991). However, to our knowledge the current study is the first to show that nest-building is directly related to condition or food availability in any bird, and contrasts with previous studies on multiple nest-building species. Longitudinal and cross-sectional analyses by Evans (1997a) suggested that nest number is a reliable indication of male body condition in European Wrens *Troglodytes troglodytes*, even when controlling for age and experience. However, a subsequent experiment involving the manipulation of nest-site availability indicated that nest number was primarily determined by habitat structure rather than male characteristics directly (Evans 1997b). In their study on Red Bishops *Euplectes orix*, Friedl and Klump (1999) also found no direct evidence that the rate of nest-building by males was related to male condition or quality. However, males that held a territory for longer and subsequently built more nests throughout the season were more likely to establish a territory in the following season, leaving open the possibility that the length of territory tenure and the number of nests built over the course of a season may reflect some aspects of male condition or quality in that species. In the European Starling *Sturnus vulgaris*, a species that uses nest-building (the addition of fresh green material to the nest) in mate attraction, nest-building is unrelated to male body size or subsequent paternal care (Brouwer & Komdeur 2004). Finally, Leonard and Picman (1987) suggested that nest number was not related to either male quality or territory quality in Marsh Wrens *Cistothorus palustris* because all males in their study ultimately built a similar number of nests; however, this is not the case in the Australian Reed Warbler.

Nest number and pairing success

In contrast to expectations, two further lines of evidence did not indicate that type II nest number

influenced pairing success. First, there was no evidence that supplementary-fed males were more successful at pairing. There were not more breeding attempts (type I nests) by area or per male in the supplementary-feeding areas, the mean distances between type I nests were very similar in supplementary-fed and control areas (indicating even distributions of nests in both areas), and there was no evidence from observations of nest attendance of colour-banded birds for increased polygyny in the supplementary-feeding areas (N. Beintema, M. Berg, & J. Welbergen unpubl. data). Secondly, the outcome of the nest-addition experiments did not support the sexual selection hypothesis: the addition of artificial type II nests to estimated 'territories' did not increase the likelihood of pairing (Fig. 3). This result also refutes further the possibility that type II nests are used to select a suitable type I nest-site, as type I nests were not more likely to be built on or in the vicinity of persisting artificial type II nests.

Research concerning the role of nest number in mate attraction in other species has yielded conflicting results. Field studies in Yellow-shouldered Widowbirds *Euplectes macrourus* (Savalli 1994), Red Bishops (Goddard *et al.* 1998, Friedl & Klump 1999) and European Wrens (Garson 1980, Evans & Burn 1996) indicate that males that build more nests have greater mating success. However, these species differ from the Australian Reed Warbler in that all nests are suitable for use by a female for breeding and appear to have an equal chance of being occupied by a female. Thus, there is a linear relationship between the number of vacant nests and apparent attractiveness to females, so these results may result from random female settlement rather than direct sexual selection on nest-building (Evans & Burn 1996, Friedl 1998). In contrast, male Marsh Wrens build clusters of nests in 'courting' centres. Females choose one of these nests or build a new nest, and males subsequently begin to build a new courting centre (Leonard & Picman 1987). In this species, Tintle (1982) and Verner and Engelsen (1970) have reported a positive correlation between male pairing success and the number of nests built over a season by males, but more recently Leonard and Picman (1987) and Metz (1991) failed to replicate these findings for reasons that remain unclear. Moreover, in the only other nest-addition experiment published to date (using natural nests), Leonard and Picman (1987) found no relationship between nest number and pairing success in Marsh Wrens.

There are at least three possible reasons why our nest-addition experiment may not have revealed a

genuine relationship between nest number and pairing success. First, owing to the extended interval between nest searches and the difficulty of detecting the precise date of pairing in such a cryptic bird, we have only considered pairing success at the end of the study period and not differences in the date of pairing. Individuals that build more type II nests may gain a fitness advantage by pairing earlier. However, as several males in the nest-addition experiment remained unpaired throughout the season, a strong effect of nest number on pairing success should still have been detected. Secondly, there is a possibility that the birds did not regard the artificial nests as genuine or that the experiment affected the behaviour of the birds in ways not measured. Our observations that a type I nest was built on top of an artificial type II nest and that material from type II nests was frequently used in the construction of type I nests (as with real type II nests) suggests at least that the former was probably not the case. Of similar studies to address these issues, Evans and Burn (1996) found that male European Wrens disregard artificially added nests, while Leonard and Picman (1987) have shown that a similar nest-addition experiment did not influence male time budgets in Marsh Wrens. Finally, the nest-addition experiment may not have revealed differences in mate attraction if the act of nest-building itself is an important component of the display. For example, male European Starlings appear to carry fresh green material to their nests for mate attraction, and males are stimulated to add such material by the experimental presence of a female (Brouwer & Komdeur 2004).

CONCLUSIONS

Previous authors on this and similar systems have suggested that multiple nest-building may be involved in mate assessment by one or both sexes (e.g. Leonard & Picman 1987, Courtney-Haines 1991, Evans & Burn 1996, Soler *et al.* 1998, Friedl & Klump 2000), and two key results in this study supported this idea. First, type II nests were built only before breeding had commenced on a territory (i.e. during mate attraction or pair formation, and not during subsequent nesting attempts). Secondly, the number of type II nests varied between territories and was positively related to food supplementation, suggesting that type II nests could provide an honest signal of the builders' condition or territory quality. However, two further lines of evidence failed to show that type II nest number was related to overall pairing success:

supplementary-fed individuals and territories with artificially added type II nests did not have a higher rate of pairing. Consequently, the function of multiple nest-building in Australian Reed Warblers remains unclear, and, on the basis of our current findings, this system warrants further study. Future work should focus on the relative contributions of each sex to the construction of type II nests, the relationships between type II nests, pairing date and other measures of reproductive investment by either parent, and the potential role of the act of building itself as an important signal.

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